Living Australian Schizasterid Echinoids

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Seven schizasterid echinoid species are recognized from Australian waters. Four of these *Schizaster (Ova) myorensis, S. (Ova) portjacksonensis, S. (Schizaster)* sp. A and *S. (Schizaster)* sp. B are new. The ontogenetic development of *S. (Ova) myorensis* is described and discussed. *Schizaster* is re-interpreted and emended. *Diploporaster* Mortensen 1951 is considered a synonym of *S. (Ova)* Gray 1825; and *Hypselaster* H. L. Clark 1917 a synonym of *Proraster* Lambert 1895.

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INTRODUCTION

The living irregular echinoids of Australia are poorly known. Since H. L. Clark's (1921, 1932, 1938, 1946) monographs, description of Australian echinoid faunas has been in abeyance. Moreover, Clark dealt largely with a few, poorly localized museum specimens. Detailed taxonomic and ecological work on the irregular echinoids is urgently needed. This paper aims to rectify the situation to a small degree by describing the schizasterid echinoids of Australia. They comprise three genera: *Schizaster, Proraster* and *Moira*. Previously (H. L. Clark, 1921, 1932, 1946; Mortensen, 1951; Endean, 1961) the only species of *Schizaster* to have been recorded from Australian waters was *S. lacunosus* (Linnaeus). We propose to show that a further four species of this genus are present, and that the distribution of *S. lacunosus* is much more restricted than hitherto considered.

Two species of *Ova,* a subgenus of *Schizaster,* are described: one from Moreton Bay, Queensland, based on relatively large, well-localized collections made by Dr. R. Endean and by Professor W. Stephenson of the University of Queensland; the other is based on two specimens collected from Port Jackson, N.S.W. and housed in the Australian Museum. In the past, species of *Schizaster* have been described on the basis of small numbers of specimens. The large collection of the Moreton Bay species has allowed a detailed description and enabled us to study both intraspecific variation within adults of the same population, and the ontogenetic development of the species. Two new species of *Schizaster* (s. s.) from northern Queensland are described. As each is known only from a single, incomplete test, open nomenclature is employed. In the light of this paper it is to be hoped that more collections will be made of the species to allow them to be named formally. In addition, H. L. Clark's (1938) "*Hypselaster dolosus*" from Western Australia is discussed and re-interpreted.

Species of *Schizaster* occur as far as 35°S on the eastern coast of Australia, but only as far south as 21° on the west. *Moira* occurs around the entire Australian coastline. *Proraster* is confined to warm seas although again extending further south on the east (27°S) than on the west (18°S).

SYSTEMATIC DESCRIPTIONS

Family SCHIZASTERIDAE Lambert, 1905

According to Mortensen (1951) and Fischer (1966) representatives of the family Schizasteridae possess both peripetalous and lateroanal fascioles. However, a number do not possess both fascioles. In *Proraster* the lateroanal fasciole may be incomplete or absent. The genus *Abatus*, which Mortensen (1951, pp. 250-251) placed in the Schizasteridae, possesses a lateroanal fasciole in the juvenile stage, but this is lost in adults. *Amphipneustes* lacks both peripetalous and lateroanal fascioles, yet is also included with Mortensen's and Fischer's Schizasteridae. In *Brisaster* the lateroanal fasciole may be reduced or lost in the adult (Mortensen, 1951, p. 280). Both *Tripylus* and *Parabrissus* possess an incomplete lateroanal fasciole; in *Parabrissus* the lateroanal fasciole is "not observed" (Mortensen, 1951, p. 348).

The work of Kermack (1954) and Nichols (1959) suggests that fascioles are not such an important taxonomic feature of spatangoids as has hitherto been considered. The genera included within Mortensen's and Fischer's Schizasteridae can be separated into groups based on a combination of morphological characters. As is discussed in more detail elsewhere (McNamara and Philip, 1980) we prefer to describe as schizasterid echinoids genera with the gross test features of *Schizaster*, *i.e.* the genera *Brisaster* Gray 1855, *Kina* Henderson 1975, *Moira* Agassiz 1872 (= *Moiropsis* Agassiz 1881), *Proraster* Lambert 1895 (= *Hypselaster* H. L. Clark 1917) and *Schizaster* Agassiz 1838 with subgenera *Dipneustes* Arnaud 1891, *Paraster* Pomel 1869, and *Ova* Gray 1825 (= *Diploporaster* Mortensen 1951). The term is therefore used in a much more restricted sense than either Mortensen (1951) or Fisher (1966). Our current revision of other fossil and living spatangoids should allow formal recognition of the group as a separate family.

Genus *SCHIZASTER* Agassiz 1836

Type Species. Schizaster studeri Agassiz 1836, p. 185; by subsequent designation of the Thirteenth International Congress of Zoology in Paris; opinion 209, 1948 (*Bull. Zool. Nomenclature* London, vol. 4, p. 527).

Emended diagnosis. Apical system located posteriorly of centre; with two to four genital pores. Ambulacrum III and anterior notch shallow to deep and with pore pairs arranged in single or double rows. Anterior petals at least twice length of posterior petals. Peripetalous and lateroanal fascioles both present and complete.

Remarks. A number of schizasterid genera have, in the past, been distinguished largely on the number of genital pores. For instance, *Schizaster* was characterized by Mortensen (1951) as possessing two genital pores, *Brisaster* three and *Paraster* four. Likewise *Diploporaster* was considered to be generically distinct from *Ova* as it possessed four genital pores, whereas *Ova* was considered to have only two; though why *Diploporaster* should have gained generic rank (Fischer, 1966) whereas *Ova* was regarded as a subgenus of *Schizaster* is unclear. Likewise *Paraster* has sometimes been considered to be only a subgenus of *Schizaster* (Kier, 1957; Henderson, 1975).

Pomel (1869) proposed *Paraster* as a genus for species previously referred to *Schizaster* which possessed four genital pores. However, whether the type species of *Schizaster, S. studeri,* has two or four genital pores remains uncertain. Cotteau (1886, p. 36) thought it had four, though Mortensen (1951, p. 287), thought it had but two. Accordingly, Mortensen characterized *Schizaster* as possessing two genital pores and *Paraster* as having four, irrespective he said, of whether or not the *S. studeri* was found to include specimens with four genital pores. Henderson (1975, p. 14) believed that *S. studeri* would "probably prove to have four gonopores" but employed *Schizaster* for species with only two.

Mortensen considered the number of genital pores to be of generic importance, even though he noted that *Abatus phillipi* Loven may equally often have two or four. Lambert and Thiéry (1924) did not use the number of genital pores as a generic character. Likewise Duncan and Sladen (1882), Currie (1925) and Cooke (1942) have considered this feature to be of only specific importance. Kier (1957) "for the sake of convenience" referred species with four genital pores to the subgenus *Paraster,* even though he noted intraspecific variation in the number of genital pores in many echinoids. More recently both Chesher (1966) and Kier (1975) have reverted to regarding forms with four genital pores as generically distinct from those with two.

The growth and development of *S. (Ova) myorensis* sp. nov. shows that at the onset of sexual maturity the posterior pair of genital pores appears first, followed, in most cases, by one of the anterior pair, then the other. However, in some specimens either one, or both, of the anterior pair may fail to develop. Consequently, most members of the population studied possess four genital pores, about 14% have three, and a similar percentage produced only two; these specimens are all large adults.

We believe, however, that it is useful to distinguish *Paraster* as a morphological subgenus of *Schizaster*, but not on the basis of the number of genital pores. Based on the morphology of the respective type species, *Paraster* is employed for species which differ from typical species of *Schizaster* s. s. in having a shallower ambulacrum III, a more circular test, a less posteriorly-situated apical system, and straighter anterior ambulacral petals which diverge more strongly. The pore pairs in ambulacrum III are set more transversely in *Schizaster* s. s. The evolutionary relationship of the subgenera is discussed elsewhere (McNamara and Philip, 1980).

Key to the Australian schizasterid genera

1. Lateroanal fasciole rudimentary or absent . . . . *Proraster*
   Lateroanal fasciole entire . . . . 2.
2. Pore-pairs in ambulacrum III in irregular double series . . . . *Schizaster (Ova)*
   Pore-pairs in ambulacrum III in regular single series . . . . 3.
3. Petals broad and open . . . . *Schizaster (Schizaster)*
   Petals narrow and very deep . . . . *Moira*

Key to the Australian species of *Schizaster*

1. Pore-pairs in ambulacrum III in irregular double series . . . . 2.
   Pore-pairs in ambulacrum III in regular single series . . . . 3.
2. Four genital pores and relatively long posterior petals . . . . *S. (Ova) myorensis*
   Two genital pores and relatively short posterior petals . . *S. (Ova) portjacksonensis*
3. Paired petals narrow, anterior pair weakly flexed distally;
   labrum short and broad . . . . *S. (Schizaster)* sp. nov. B
   Paired petals broad . . . . 4.
4. Anterior petals strongly flexed distally . . . . *S. (Schizaster)* sp. nov. A
   Anterior petals not flexed distally . . . . *S. (Schizaster) lacunosus*

Subgenus *SCHIZASTER* Agassiz 1836

Diagnosis. Pore pairs in ambulacrum III arranged in regular single series in both juvenile and adult stages.

Schizaster (Schizaster) lacunosus (Linnaeus 1758)

(Fig. 1)

Material and locality. A single, complete specimen (WAM 1488.75) dredged from a depth of 4-5 m outside Norbill Bay, Rosemary Island, Dampier Archipelago, Western Australia and an incomplete specimen (MCZ 6066) from the lee of Turtle Island at 8 fathoms, collected on the Great Barrier Reef Expedition 1928-29.

Description. Test length of W.A. specimen 23.5 mm; test broad, maximum width 87.5% test length, and high, maximum height 65.4% test length. Apical system with

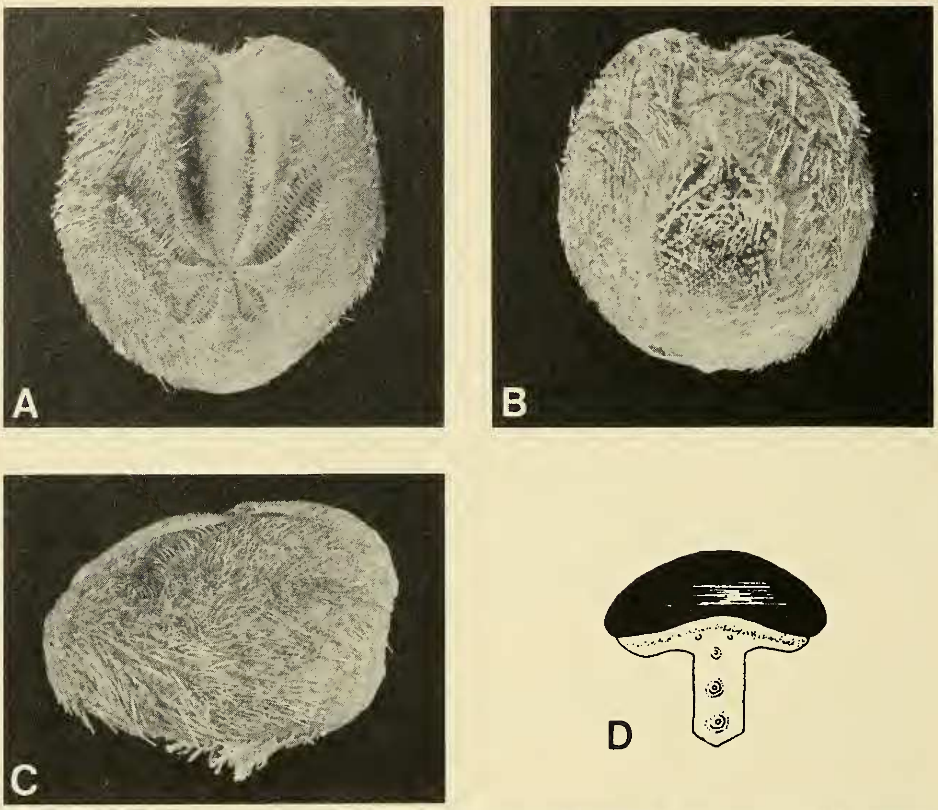


Fig. 1. Schizaster (Schizaster) lacunosus (Linnaeus 1758) WAM 1488.75, from Norbill Bay, Rosemary Island, Dampier Archipelago, Western Australia. **A**, aboral view; **B**, adoral view; **C**, lateral view; all x2. **D**, labrum of *Schizaster (Schizaster) lacunosus* (Linnaeus 1758) WAM 1488.75. x7.

two genital pores, situated 57.5% test length from anterior margin. Ambulacrum III broad and deep, with 29 pore pairs arranged in single series. Anterior notch broad and moderately indented. Anterior petals progressively widen adapically, reaching a maximum width of 11.5% test length; not reflexed distally; diverging at approximately 85°. Posterior petals broad and short, one third length of anterior petals. Interambulacra 2 and 3 forming keels adapically. Peripetalous fasciole broad and extending to 9% test length from apical system in interambulacrum 1. Lateroanal fasciole narrow and passing 11% test length below periproct.

Plastron narrow, occupying 46% width of test. Labrum very narrow and long posteriorly (Fig. 1D); anteriorly acuminate medially and projecting sharply anteroventrally; anterior of labrum situated 17% test length from anterior margin of test. Peristome wide, 22.5% test length.

Discussion. This species has previously been recorded in Australian waters from Madge Reefs, Thursday Island, Queensland (Clark, 1921, p. 153) and from Turtle Isles in the Great Barrier Reef (Clark, 1932, p. 219). The record from Madge Reefs (MCZ 4147) comprises two broken specimens, neither of which is *S. (Schizaster) lacunosus*, one being an indeterminate species of *S. (Ova)*, the other being *Proraster jukesii*. The Turtle Island specimen is, however, confirmed as being *S. (Schizaster) lacunosus*, and consequently represents the only known example of this species from eastern Australia.

H. L. Clark (1946, p. 368) considered that *S. lacunosus* was absent from Western Australia, being replaced by *"Hypselaster dolosus"*. The specimen of *S. (Schizaster) lacunosus* from Rosemary Island extends the known range of *S. (Schizaster) lacunosus* from the Japan and China seas (Mortensen, 1951, p. 303) to Western Australia. A. M. Clarke and Rowe (1971, p. 149) question the accuracy of Mortensen's (1951, p. 303) record of *S. (Schizaster) lacunosus* from the Maldives; thus the species is probably restricted to the western Pacific region and Queensland. The specimen from Natal, South Africa referred to *S. (Schizaster) lacunosus* by Mortensen (1951, p. 303, Pl. 21, figs 5, 6) differs from typical specimens of *S. (Schizaster) lacunosus* in its more posteriorly located apical system, relatively shorter petals, less anteriorly divergent petals and longer ambulacrum III.

Schizaster (Schizaster) sp. nov. A.

(Figs 2A-C, 3A)

Material and locality. A single specimen, QM G2178, from North Keppel Island, Queensland.

Diagnosis. Test moderately depressed, with deep, but broad anterior notch; test vertically truncated posteriorly. Apical system posteriorly located about two-thirds test length from anterior; bears four genital pores. Ambulacrum III deep and broad, with steep sides. Anterior petals broad and strongly curved; posterior petals short and broad. Labrum long and narrow.

Description. Test is large (test length 63.5 mm); width of test 88% its length; test height 58.5% test length. Test highest posterior to apical system at keel of interambulacrum V (Fig. 2C). Posterior face of test almost vertical. Apical system ethmolytic, depressed, with four genital pores, posterior pair being much larger than anterior pair. Ambulacrum III long, deep and wide (13.3% test length); pore pairs arranged in a single row. Outer pores elongate and larger than inner pores. Anterior notch broad and deep. Interambulacra II and III form sharp, high keels. Anterior petals strongly flexuous and broad (Fig. 2A), being 10.5% test length wide and bearing pore pairs which are subcircular, widely spaced and conjugate; 38 pairs are

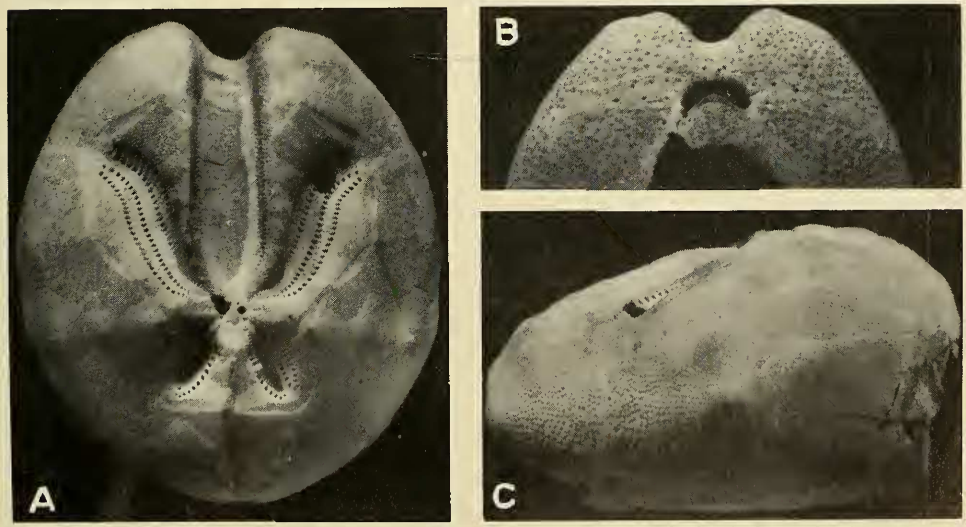


Fig. 2. Schizaster (Schizaster) sp. nov. A, QM G2178, from North Keppel Island, Queensland; **A**, aboral view; **B**, adoral view of anterior part of test; **C**, lateral view; all x1.

present. Posterior petals moderately long (occupying 16.5% test length) and broad, bearing 23 pore pairs.

Peripetalous fasciole transverse posteriorly; in form like that of *S. (Ova) myorensis*. Lateroanal fasciole extends in a straight line across posterolateral part of test, extending close to ambitus posteriorly. Peristome hardly sunken; anterior tip of labrum set 17.5% test length from anterior and projecting anteriorly. Labrum with anterior rim poorly developed; medially acuminate; posteriorly long, narrow and parallel-sided (Fig. 3A); covered by small tubercles anteriorly and by larger ones posteriorly. Plastron incompletely known, but thought to have been rather narrow, width being approximately 70% of the length.

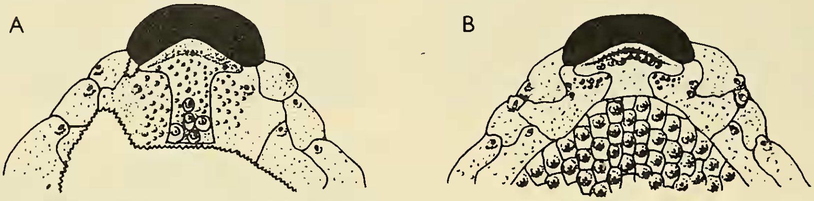


Fig. 3. Labrum and adjoining ambulacral plates of, A, *Schizaster (Schizaster)* sp. nov. A, QM G2178, from North Keppel Island, Queensland, x2. B, *Schizaster (Schizaster)* sp. nov. B, QM G12092, from Stone Island, Edgecumbe Bay, Queensland, x2.

Discussion. S. (Schizaster) sp. nov. A compares closely with the specimen from South African waters figured by Mortensen (1951, Pl. 21, figs 5, 6) and referred by him to *S. (Schizaster) lacunosus* (see above). However, it differs in possessing a more parallel-sided ambulacrum III, more strongly reflexed anterior petals, and by its possession of an anterior pair of genital pores, in addition to the large posterior pair. *S. (Schizaster)* sp. nov. A differs from *S. lacunosus* in possessing a greater number of genital pores, more distally reflexed and less divergent anterior petals, deeper anterior notch and broader labrum. *S. (Schizaster) edwardsi* Cotteau, from the Gulf of New Guinea (Mortensen, 1951, Pl. 21, figs 1-4, ?11-13) is similar to the Queensland species, but has only two genital pores, a more posteriorly positioned peristome and a constricted labrum.

Schizaster (Schizaster) sp. nov. B
(Figs 3B, 4A-D)

Material and locality. A single specimen QM G12092 collected by Dr. E. Frankel from the spit at the southern end of Stone Island, Edgecumbe Bay, Queensland.

Diagnosis. Paired petals narrow, anterior pair relatively straight; posterior pair long, half length of anterior pair. Anterior notch deep and narrow. Apical system only slightly posterior of centre, with four genital pores. Labrum very short and broad, projecting only weakly anteriorly; anterior rim poorly developed.

Discussion. S. (Schizaster) sp. nov. B differs from *S. (Schizaster)* sp. nov. A in possessing straighter, narrower anterior petals; longer (22.2% test length compared with 16.4%), narrower posterior petals; a more centrally located apical system; a shorter, broader labrum (Fig. 3B); and a broader plastron. The lateroanal fasciole follows the contours of the test more closely in *S. (Schizaster)* sp. nov. B initially, before it bends through 90° close to the posterior of the test to run ventrally and pass below and close to the periproct.

S. (Schizaster) sp. nov. B can be distinguished from *S. (Schizaster) lacunosus* by its apical system, which bears four genital pores, unlike *S. (Schizaster) lacunosus* which only has two. Although broken, the apical system of *S. (Schizaster)* sp. nov. B

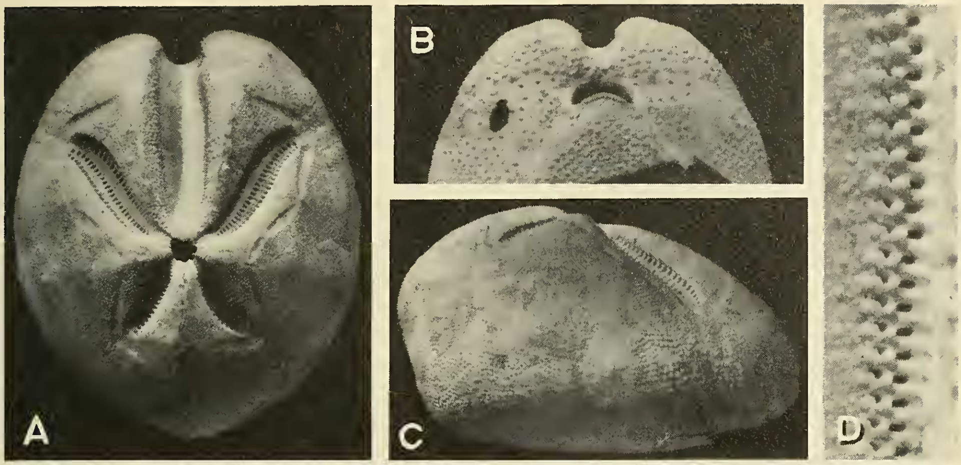


Fig. 4. Schizaster (Schizaster) sp. nov. B, QM G12092 from Stone Island, Edgecumbe Bay, Queensland; **A**, aboral view; **B**, adoral view of anterior part of test; **C**, lateral view; all x1; **D**, pore pairs of ambulacrum III, x8.

shows the outer part of a large posterior pore and a smaller anterior pore, indicating the possession of four genital pores. *S. (Schizaster)* sp. nov. B can further be distinguished by its narrower paired petals and deeper anterior notch, longer posterior petals, more distally reflexed anterior petals and broader labrum.

Subgenus *OVA* Gray 1825

Emended diagnosis. Species of *Schizaster* with pore pairs in ambulacrum III arranged in irregular double series in adult stage.

Remarks. H. L. Clark (1917, 1925) resurrected Gray's (1825) *Ova* for *Spatangus canaliferus* Lamarck 1816. Although Mortensen (1951, p. 308) recognized that the nature of the poriferous tract of ambulacrum III precluded placing *canaliferus* in *Schizaster,* he preferred to regard *Ova* as a subgenus of *Schizaster,* a course followed by Fischer (1966, p. U569). Within the various *Schizaster*-like forms from eastern Australia, the pores form either a distinct single series or a very irregular double series. The juvenile stage of *Ova* possesses a single row of pores, like *S. (Schizaster);* the irregular double row develops with growth in the adult stage of *Ova,* but remains single in *Schizaster.* Mortensen and Fischer are herein followed in regarding *Ova* as a subgenus of *Schizaster,* as its single differentiating character only appears in the adult stage.

The number of genital pores is thought not to be a generic characteristic of the Schizasteridae; likewise the nature of the pore pairs is thought to be of less than generic significance.

Schizaster (Ova) myorensis sp. nov.
(Figs 5A-E, 7A-C, 8A-C, 9A)

1961 *Schizaster lacunosus* Linnaeus; Endean, p. 294

1978 *Schizaster lacunosus* Linnaeus; Stephenson *et al.,* p. 207.

Holotype. QM G12063 from Myora, Moreton Bay, Queensland.

Paratypes. QM G3870-1, 11826-8, 12064-6, 12094, 12428-45 from Myora, Moreton Bay, Queensland, QM G11826-8, 12065-6, 12446-8 from Middle Banks, Moreton Bay, Queensland and QM G3809 from Dunwich, Moreton Bay, Queensland.

Material and localities. Forty one specimens are available for this study, ranging in size from a test length of 7.0 mm to 71.2mm; only twenty eight were undamaged and could be measured. Six of the specimens were in a pre-adult stage, the remainder are adults. Thirty of the specimens were collected by Dr. R. Endean in 1960 from sandy mud near the "Black Beacon" at Myora in Moreton Bay. Dr. Endean (pers. comm. 26.9.78) informs us that the specimens were dug from burrows, which extended to 10 cm below the surface of the intertidal flat, approximately L.W.N. to L.W.S. One specimen was found burrowing in muddy sand at L.W.N. at Dunwich in Moreton Bay. Nine specimens were collected by Professor W. Stephenson in 1972 from sites 34, 43, and 51 on Middle Bank, Moreton Bay (Stephenson *et al.,* 1978, Fig. 2). Professor Stephenson (pers. comm. 19.9.78) informs us that site 34 was at a depth of 11±2 fathoms; sites 43 and 51 at 15±2 fathoms. The depth of burial of the specimens is not known. This species forms part of the *Schizaster — Nucula — Prionospio* community of Stephenson *et al.* (1978, p. 199). This community occurs in the south-western part of Middle Banks, where the sediment has the highest mud content found in the area (16% mud and 76% fine sand).

Diagnosis. Anterior ambulacral petals long and flexuous; posterior petals long. Interambulacra strongly keeled adapically. Apical system with two to four genital pores. Peristome situated well back from anterior of test. Labrum projects strongly forward; moderately broad and parallel-sided posteriorly.

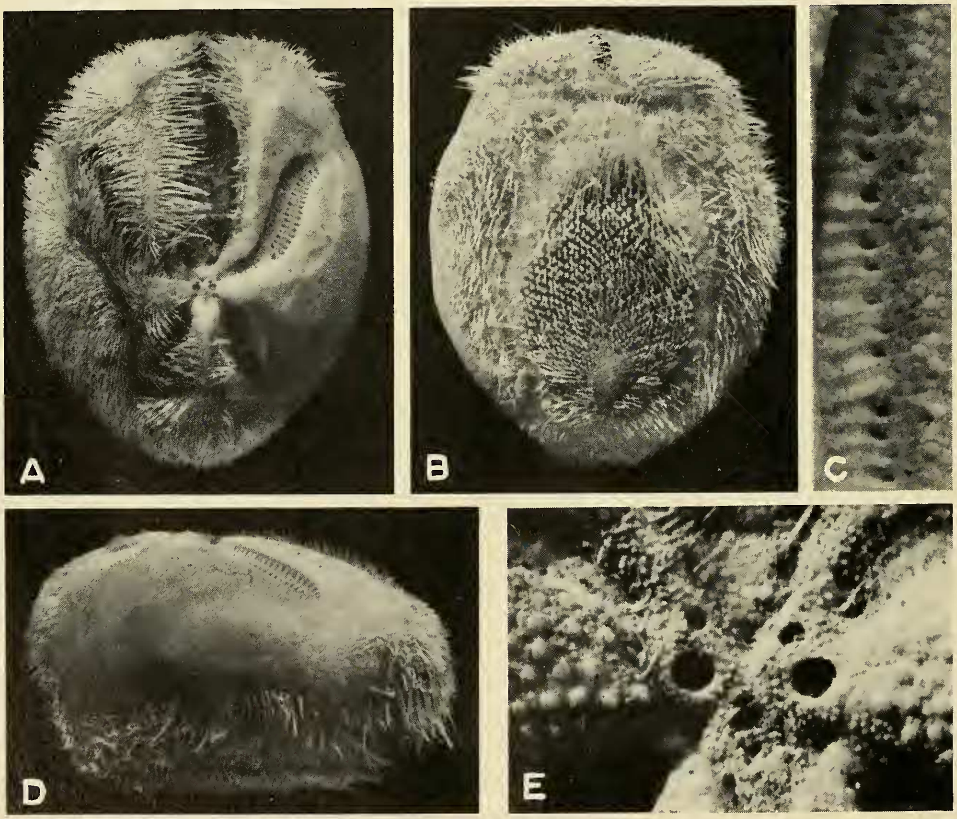


Fig. 5. Schizaster (Ova) myorensis sp. nov. A, B, D, aboral, adoral and lateral views, respectively, of holotype, QM G12063 from Myora, Moreton Bay; all x1; C, irregular double pore pairs of ambulacrum III, QM G12094, paratype, from Myora, Moreton Bay, x7. E, apical system of QM G3809, paratype, from Dunwich, Moreton Bay, x8.

Description. The test, which reaches a maximum known test length of 71.2 mm, is very variable in shape. Although being always longer than broad, there is up to 15% variation, width of test varying in adults between 74% and 91% of test length (Fig. 6B). Similarly maximum height of test varies, being between 53% and 63% of test length in adults (Fig. 6A). Widest part of test is at half test length; highest part of test is posterior to apical system, at about 25% test length from posterior. Aboral surface declines anteriorly at 15°. Posteriorly keeled interambulacrum V overhangs periproct. Anteriorly a deep notch is present in test. Apical system is depressed and set posterior of centre, between 55% and 62% of test length from anterior; ethmolytic. Of thirty five adult specimens studied, twenty six possess four genital pores, four had produced only three, while five specimens have only two. Posterior pair of genital pores are larger and more widely spaced than anterior pair. Smaller anterior pair may be set close to, and conjoined with, the posterior pair (Fig. 5E). Madreporite long, extending past posterior oculars. Ocular plates are triangular.

Ambulacrum III is long, deep and wide. From apical system it declines steeply anteriorly initially and progressively widens; it reaches its maximum width (12% to 20% of test length) and maximum depth at mid-length; rises gently and constricts a little anteriorly to deep anterior notch; it is sunken to peristome. Slightly obliquely orientated pore pairs are arranged in an irregular double series (Fig. 5C). The outer pores of the series are tear-shaped. The outermost pore is large, whilst its partner is small and shallow. Both are surrounded by a narrow, raised rim. Pores are conjugate but separated by a swollen interporal partition. The inner pore pairs of the double series are smaller than outer pores; they are equidimensional. Ambulacral plates often occluded in region of poriferous zone. Pore pairs form a single series abapically close to where peripetalous fasciole meets ambulacrum III. Anterior to this there are only four single pores to peristome. Funnel-building tube feet not fully developed close to apical system; fully developed tube feet densely concentrated toward the peripetalous fasciole and bearing discs which carry approximately twenty papillae.

Ambulacra II and IV aborally petaloid, sunken, long and sinuous, being reflexed distally. They occupy a length of between 40% and 46% of test length (measured in a straight line from apical system to abapical extremity of petal). Number of pore pairs variable, ranging from 33 to 47 in adults from 40 mm to 60 mm test length, respectively. Pore pairs transverse to axis of petal; conjugate; each pore separated by width equal to diameter of three pores. Pores contain simple respiratory tube feet. Interporiferous zone equal in width to that of poriferous zone. Petals overhung adapically by interambulacra. Width of petals 8% to 13% of test length; angle of divergence approximately 80°; distance between abapical extremities 48% to 58% test length.

Ambulacra I and V aborally petaloid, sunken, straight and up to one-half length of anterior paired petals. They occupy a length of between 16% and 23% of test length in adults. Number of pore pairs ranges between 19 and 27 in specimens of test length 40 mm to 60 mm, respectively. Form of pore pairs like those of anterior paired petals. Petal width varies between 7% and 11% of test length. They diverge posteriorly at approximately 75%. Distance between abapical extremities of petals is 25% to 35% of test length.

Peripetalous fasciole runs transversely between posterior petals, thickening at petal extremities and running forward exsagittally until in line with apical system, before bending outward toward extremities of anterior petals. Between anterior and posterior petals fasciole constricts three times: at outward flexure near apical system; where fasciole joined by lateroanal fasciole at about mid-test length; and midway between those two points. These constrictions occur in the centre of interambulacral

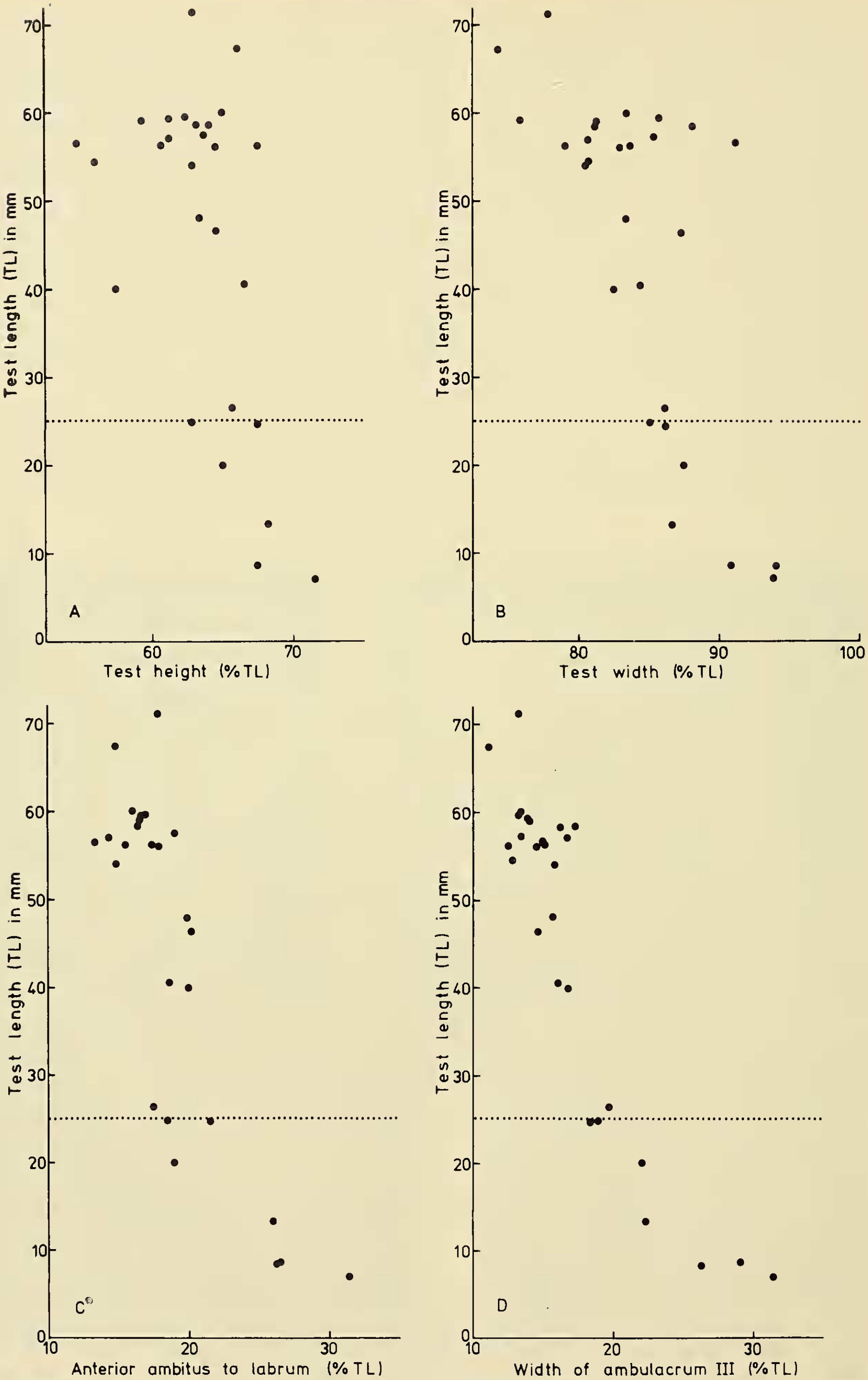


Fig. 6. Plots of test length against test height (**A**), test width (**B**), sagittal length from anterior ambitus to labrum (**C**) and width of ambulacrum III (**D**) of *Schizaster (Ova) myorensis* sp. nov. expressed as percentages of test length; broken line represents test length at attainment of sexual maturity.

plates where plates form a raised point (Fig. 5A); all interambulacral plates are similarly raised centrally. Peripetalous fasciole runs forward from anterior petals at about 45° before curving more strongly forward close to its junction with ambulacrum III, which it meets at 12% test length from anterior of test. One specimen (QM G3809) has a curious posterior extension of the peripetalous fasciole extending sagitally posterior from between the posterior petals for 10% test length.

Lateroanal fasciole narrower than peripetalous and of more constant width. From peripetalous fasciole it extends abaxially posteriorly at 30° to an exsagittal line; close to ambitus it recurves sharply and runs straight toward periproct. On meeting posterior petals it bends to run far below periproct, close to adoral surface. Area between periproct and lowest part of lateroanal fasciole forms a shallow depression.

Peristome oval and slightly sunken; situated anteriorly, anterior tip of labrum 13% to 19% test length from anterior of test in adults. Peristomial girdle is composed of four large, pentagonal plates anteriorly, interdigitating with three shorter plates posteriorly. Laterally there are many small plates. Anteriorly labrum strongly curved and projects forward strongly; bounded by thick rim which degenerates laterally. Labrum (Fig. 9A) as long as broad, posterior extension being rectangular and more than twice as long as broad. Labrum carries large tubercles medially; these decrease in size anteriorly and laterally. Labrum does not extend beyond first adjacent ambulacral plate. Oral tube feet are arranged in a phyllode; eight are borne in each of ambulacra II and IV. Ambulacra I and V each bear nine; pores single within phyllode. Posteriorly eight tube feet occur in ambulacra I and V below periproct. Plastron oval and broad, maximum width being three-quarters length. Plastron tubercles are regularly arranged in curving rows which extend postero-laterally adaxially at a high angle anteriorly, and at a progressively smaller angle posteriorly.

Within anterior and posterior paired ambulacra, and scattered on the surface of interambulacra, are globiferous pedicellariae (Fig. 7A). They consist of three, cylindrical, gently curving valves which are narrowest distally where they bear eight very small denticles; gradually widen toward base initially; at half length broaden strongly to become four times wider at base than at tip; skeletal material dense. Within ambulacra I and V on adoral surface, quadridentate pedicellariae (Fig. 7B) are common. They occur rarely within the ambulacra on the aboral surface. The four, almost straight, valves are broad basally, but rapidly narrow to one-fifth this width at a little over one-third valve length. For the most part the valve is parallel-sided, but restricted broadening occurs near mid-length and distally, the tips being spatulate. Valves are strongly denticulate marginally from median thickening close to spatulate tip. Around margin of spatulate tip, very small, densely packed denticles are present. These probably serve to hold valves tightly together. The skeletal structure of this pedicellaria is an open meshwork, much in contrast to the dense structure of the globiferous pedicellariae. Within ambulacrum III on aboral surface, rostrate pedicellariae (Fig. 7C) occur on upper sides of ambulacral walls. Valves are similar in size to those of the quadridentate pedicellariae, and basally are of similar form. However, the rostrate valves lack the median thickening, are strongly curved distally and do not possess denticulate margins.

Ontogeny. The smallest known specimen is one of test length 7.0 mm (Fig. 8A-C). Other specimens are known of test lengths 8.4 mm, 8.6 mm and 12.5 mm. The onset of maturity is taken as being indicated by the opening of the genital pores. A specimen 20.0 mm test length has just the posterior pair of pores open. In a specimen 24.8 mm test length a third pore is just open, whilst specimens 24.6 mm and 26.5 mm test length have all four pores open. Thus it would appear that the genital pores had opened by a test length of approximately 25 mm in length, although, as noted above,

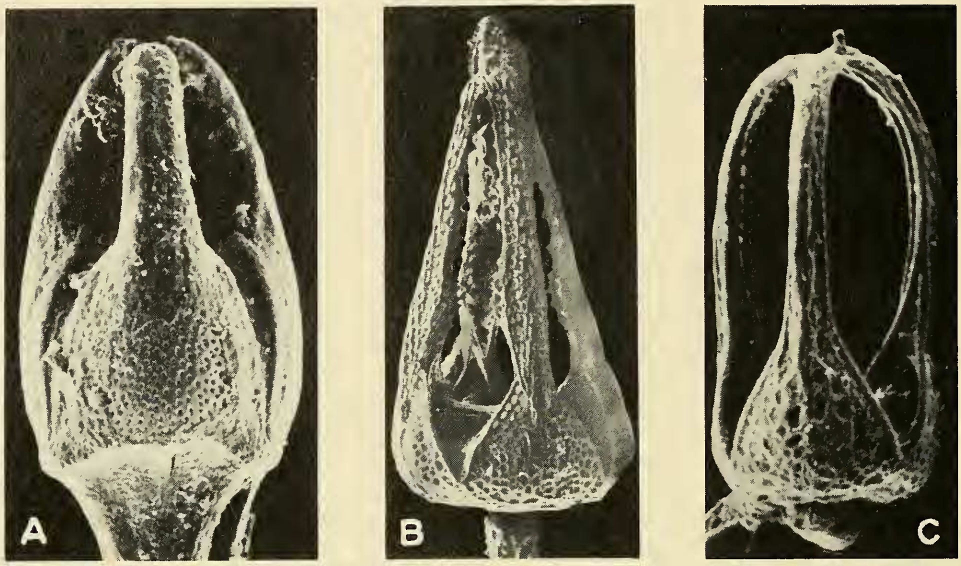


Fig. 7. Pedicellariae of *Schizaster (Ova) myorensis* sp. nov., QM G12064, paratype, from Myora, Moreton Bay: **A**, globiferous, x65; **B**, quadridentate, x100; **C**, rostrate, x100.

nine adult specimens, ranging in test length between 48.0 mm and 58.5 mm have not formed all four genital pores.

The proportions of many morphological features differ between juveniles and adults, and may show negative, normal or positive allometry. In juveniles ambulacrum III is relatively very wide aborally, being up to 31.5% of the test length. It shows negative allometry with growth of the test, becoming relatively narrower, such that it is only between 12% and 20% of the test length in adults (Fig. 6D). The widths of the paired ambulacra remain virtually constant relative to growth of the test. The test itself shows a small change in shape with growth (Fig. 6A, B), juveniles being higher and broader than adults, i.e. it becomes less spherical with growth.

The paired petals change both in shape and orientation with growth. The width between the anterior petals is almost 60% of the test length in juveniles, but decreases to between 46% and 58% in adults. Greater change occurs in the disposition of the posterior petals. In juveniles the width between the extremities of the petals may be as little as 15.5% of the test length, whereas in adults it may range up to 35%, although can be as low as 25%. The anterior petals become more sinuous with growth, juveniles lacking the distal reflexion. The number of pore pairs appears to increase progressively with growth at a constant rate. The peristome is proportionately wider in juveniles, being as much as 22.5% of the test length; in adults it varies between 11% and 16%, illustrating negative allometry with growth of the test (Figs 5A, 8A). The periproct grows with normal allometry. The peristome also moves forward with growth, the anterior of the labrum being up to 31.5% of the test length from the anterior in juveniles, but only 13% to 19% in adults (Fig. 6C). This change is also due, in part, to an increase in anterior projection of the labrum over the peristome. During growth the apical system moves relatively closer to the posterior (Figs 5A, 8A). The increased sinuosity with growth of the anterior paired petals may indicate increased rate of production of ambulacral plates in adults. This is also evident in ambulacrum III. In juveniles the pore pairs occur in a single row. However, in young adults, i.e. those below test length of 40 mm, the pore pairs start to form a more

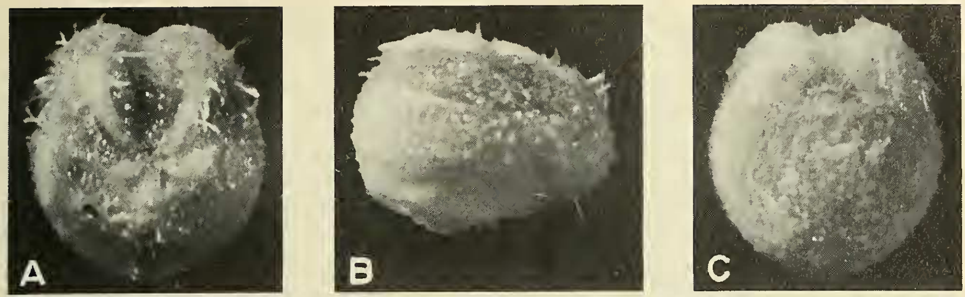


Fig. 8. Juvenile *Schizaster (Ova) myorensis* sp. nov., QM G12066, from Middle Bank, Moreton Bay; **A**, aboral view; **B**, lateral view; **C**, adoral view; all x5.

irregular series, such that in larger adults 60 mm test length, two irregular rows are discernible (Fig. 5C). Occlusion of plates also occurs in adults, probably so that more ambulacral plates could fit into the length of ambulacrum III.

The only observable change in the form of the fascioles is a relative increase in width of the peripetalous fasciole. The lateroanal fasciole, which is similar in width to the peripetalous in juveniles, but narrower in adults, shows negative allometry with growth of the test in comparison with the peripetalous fasciole. This suggests that the lateroanal fasciole assumed greater importance in juveniles than the peripetalous fasciole; but that with growth this situation is reversed.

Fig. 6 shows the more rapid morphological changes which occur up to a test length of less than 25 mm; this corresponds with the opening of the genital pores suggesting onset of sexual maturity.

Discussion. The specimens described here as *S. (Ova) myorensis* were originally assigned to *S. (Schizaster) lacunosus* (Linnaeus) by Endean (1961) and by Stephenson *et al.* (1978). Indeed, in the past it seems to have been common practice to call any *Schizaster*-like form from eastern Australia *'Schizaster lacunosus'* (Clark, 1921, 1932, 1946; Mortensen, 1951). *S. (Schizaster) lacunosus* is best restricted to the specimens from Japan and the southern Pacific, as discussed by Mortensen (1951, pp. 300-303) and the Australian specimens mentioned above. *S. (Schizaster) lacunosus* is more circular in outline than other Australian species. It possesses single rows of pore pairs in ambulacrum III which is not as deep as that of *S. (Ova) myorensis.* It also has shorter, straighter petals and a much narrower labrum.

S. (Ova) myorensis is morphologically closest to *S. (Ova) savignyi* (Fourtau, 1904, pp. 436-439, Pl. 1, figs 4-5) from the Red Sea. Both possess four genital pores in addition to the irregular double row of pore pairs in ambulacrum III. *S. (Ova) myorensis* can, however, be distinguished by the possession of longer paired petals with more pore pairs. According to Fourtau (1904, p. 437) a specimen of *S. (Ova) savignyi* of test length 53.5 mm possesses 33 pore pairs in each of the anterior petals, and 17 in each of the posterior pair. In a Moreton Bay specimen of comparable test length there are 40 pore pairs anteriorly and 23 posteriorly. The longer petals of *S. (Ova) myorensis* result in a different fasciole pattern; the anterolateral branch of the peripetalous fasciole is more transversely orientated in *S. (Ova) myorensis,* whilst the posterolateral is more nearly exsagittal. The section of the peripetalous fasciole which links the posterior petals is virtually transverse in *S. (Ova) myorensis,* but posteriorly convex in *S. (Ova) savignyi.* Ambulacrum III appears to be a little wider in *S. (Ova) myorensis* than in the illustrated specimens of *S. (Ova) savignyi* (Fourtau, 1904, Pl. 1, fig 4; Koehler, 1914, Pl. 8, fig. 13). Mortensen (1951, p. 242) says that the double row of pore pairs in ambulacrum III appears in *S. (Ova) savignyi* in specimens only 20 mm test length, this specimen possessing four genital pores. *S. (Ova) myorensis* does not attain all its adult number of genital pores until 25 mm test length, and in specimens of this length the pore pairs in ambulacrum III form a single row. In a specimen of *S. (Ova) myorensis* of test length 40 mm the poriferous zone has just started to form an irregular double series. Mortensen also noted how the keels of interambulacra II and III overhang ambulacrum III in *S. (Ova) savignyi,* so as to almost cover the poriferous zone when viewed from above; the same keels in *S. (Ova) myorensis* do not overhang to the same extent, the poriferous zones being completely visible. In contrast to Koehler's figured specimen, *S. (Ova) myorensis* possesses far more strongly keeled interambulacra aborally. In addition, the peristome is more anteriorly placed in *S. (Ova) savignyi,* whilst the anterior part of the labrum is much less prominent than in *S. (Ova) myorensis.* Posteriorly the labrum of *S. (Ova) savignyi* appears narrower than that of *S. (Ova) myorensis.* The posterior pair of genital pores appear relatively much smaller in *S. (Ova) savignyi* than in *S. (Ova) myorensis,* and are more widely spaced (Koehler, 1914, Pl. 8, fig. 6). In contrast to Koehler's specimen, the interambulacra of *S. (Ova) myorensis* are far more strongly keeled adapically.

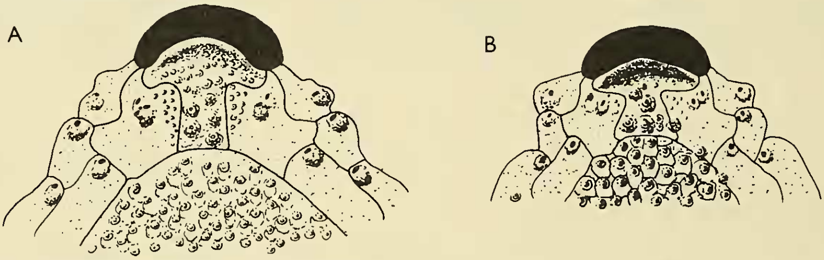


Fig. 9. Labrum and adjoining ambulacral plates of, **A**, *Schizaster (Ova) myorensis* sp. nov. QM G3809, paratype, from Dunwich, Moreton Bay, x2.5. **B**, *Schizaster (Ova) portjacksonensis* sp. nov., AM J1732, holotype, from Port Jackson, N.S.W., x2.

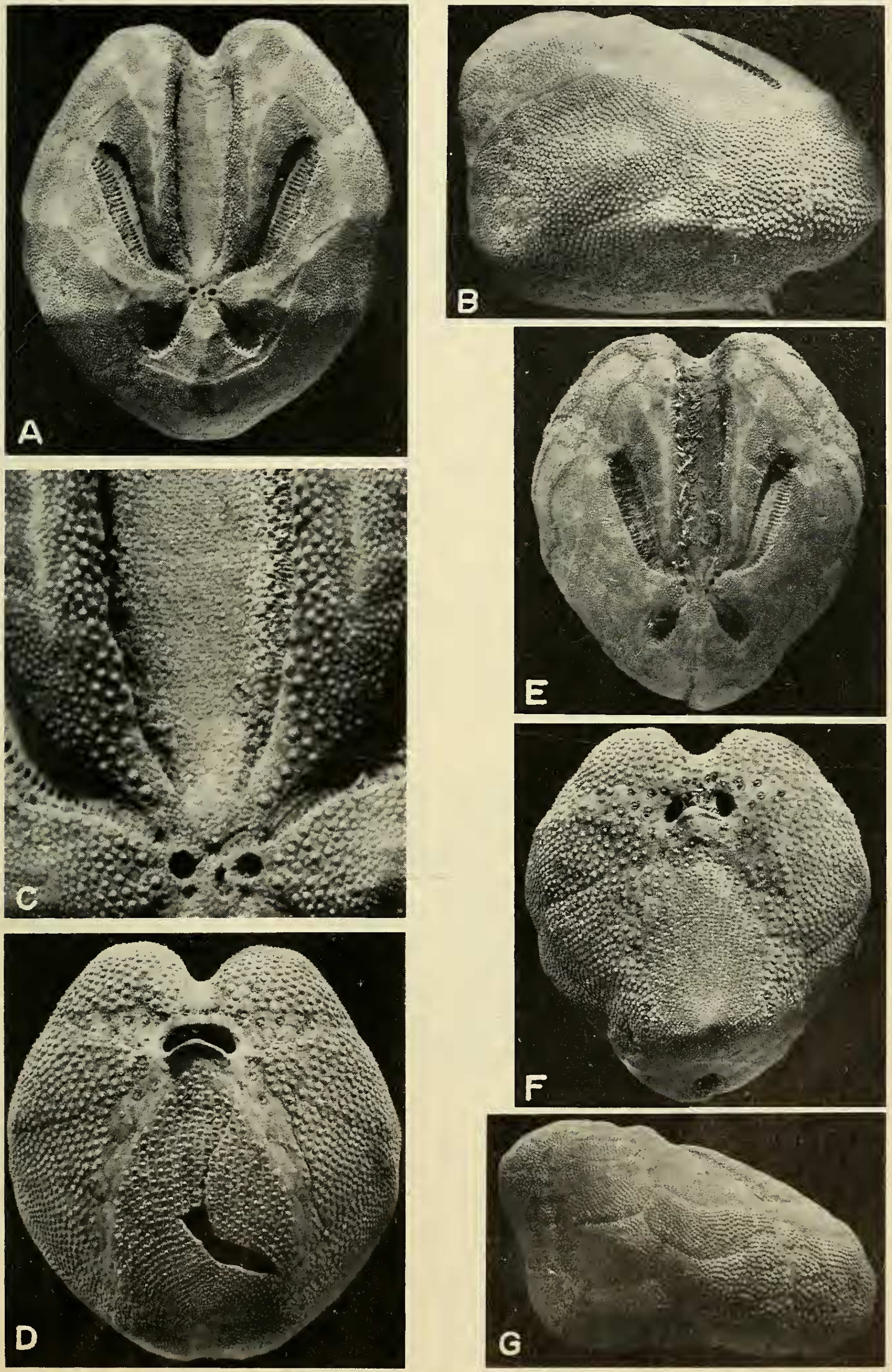
S. (Ova) canaliferus from the Mediterranean, differs from *S. (Ova) myorensis* in the following characters: straighter anterior petals; shorter posterior petals; only two genital pores; smaller outer pores in ambulacrum III; broader labrum which has a more pronounced anterior rim; and a narrower plastron. *S. (Ova) barbatus* (Mortensen, 1951), known from a single specimen from Tanzania, has straighter anterior petals and shorter, more divergent posterior petals than *S. (Ova) myorensis.* The test of *S. (Ova) barbatus* (Mortensen, 1951, Pl. 25, figs 1-3) is also much flatter than that of *S. (Ova) myorensis.* Comparison with *S. (Ova) portjacksonensis* is made in discussion of that species.

Schizaster (Ova) portjacksonensis sp. nov.
(Figs 9B, 10A-G)

Type specimens. Holotype: AM J1732; *paratype:* AM J1731; both collected from 'Port Jackson' and now housed in The Australian Museum. Information on the label gives the depth at which the specimens were collected as 7 fathoms. These are the only known specimens.

Diagnosis. Short, broad, widely spaced posterior petals. Apical system with two genital pores. Anteriorly labrum projects strongly ventrally; it is short, constricted medially. Tubercles on adoral surface densely packed.

Fig. 10. Schizaster (Ova) portjacksonensis sp. nov. from Port Jackson, N.S.W.; **A**, aboral view; **B**, lateral view; **C**, apical region, x3.5; **D**, adoral view, of AM J1737, holotype. **E**, aboral view; **F**, adoral view; **G**, lateral view of AM J1731, paratype. All x1 except where otherwise stated.


A
B
C
D
E
F
G

Discussion. S. *(Ova) portjacksonensis* is morphologically most similar to S. *(Ova) canaliferus.* Both share a strongly inflated test and similar aboral morphology. However, S. *(Ova) portjacksonensis* has a more posteriorly placed apical system (varying between 56.5% and 59.1% of the test length from the anterior, whilst in S. *(Ova) canaliferus* it varies only between 50.8% and 53.7%). The posterior petals diverge more strongly in S. *(Ova) portjacksonensis* than in S. *(Ova) canaliferus,* though not reaching the depth of S. *(Ova) myorensis.* S. *(Ova) portjacksonensis* can be more easily distinguished from S. *(Ova) canaliferus* by the morphology of the adoral surface of the test. The plastron of S. *(Ova) portjacksonensis* is broader than in S. *(Ova) canaliferus* (0.83 the length compared with 0.68). The labrum of S. *(Ova) portjacksonensis* (Fig. 9B) anteriorly projects more strongly ventrally and is medially acuminate; posteriorly the labrum is constricted medially, unlike S. *(Ova) canaliferus* in which it is parallel-sided. It is proportionately shorter in S. *(Ova) portjacksonensis.* The adoral tubercles are more dense in S. *(Ova) portjacksonensis* than in either S. *(Ova) canaliferus* or S. *(Ova) myorensis.*

S. *(Ova) portjacksonensis* possesses a more inflated test than S. *(Ova) myorensis*; its paired petals are shorter, the anterior pair being less flexuous anterolaterally. S. *(Ova) myorensis* possesses more genital pores than S. *(Ova) portjacksonensis* and has a deeper ambulacrum III. The interambulacra do not form such prominent keels adapically in S. *(Ova) portjacksonensis.* The labrum projects ventrally (Fig. 10B), not anteriorly as in S. *(Ova) myorensis,* and is medially constricted, unlike S. *(Ova) myorensis* which is parallel-sided. The adoral tubercles of S. *(Ova) portjacksonensis,* in addition to being more densely packed than in S. *(Ova) myorensis,* are larger; this is also true of the aboral surface. The few spines preserved in the ambulacra of S. *(Ova) portjacksonensis* are like those of S. *(Ova) myorensis.*

The paratype of S. *(Ova) portjacksonensis* (Fig. 10E-G) possesses a much less inflated test than the holotype. However, this variation comes within the limits of variation in test shape displayed by S. *(Ova) myorensis.* This paratype is a

TABLE 1

Dimensions (in mm) of typical specimens of the four new Australian species of *Schizaster* discriminated in this paper. In brackets the various parameters are given as a percentage of test length.

	S. (Ova) myorensis QM G12063 (holotype)	*S. (Ova) portjacksonensis* AM J1732 (holotype)	*S. (Schizaster)* sp. nov. A QM G2178	*S. (Schizaster)* sp. nov. B QM G12092
Test length	57.0	60.5	64.0	54.0
Test width	46.0 (81.0)	54.0 (88.5)	56.0 (87.5)	46.5 (86.0)
Test height	35.0 (61.5)	43.0 (71.0)	38.0 (59.5)	33.0 (61.0)
Length apical system to anterior	33.0 (58.0)	35.0 (58.0)	37.5 (58.5)	30.0 (55.5)
Width amb. III	9.5 (16.5)	8.7 (14.5)	8.5 (13.5)	6.5 (12.0)
Width amb. I/V	4.7 (8.0)	4.4 (7.5)	4.5 (7.0)	4.0 (7.5)
Width amb.II/IV	5.3 (9.5)	5.0 (8.5)	6.0 (9.5)	4.3 (8.0)
Width ant. paired petals	30.7 (54.0)	32.0 (53.0)	33.0 (51.5)	30.0 (55.5)
Width post. paired petals	15.5 (27.0)	15.4 (25.5)	16.0 (25.0)	16.3 (30.0)
Length amb. II/IV	(36.5)	(41.0)	(37.5)	(37.0)
Length amb. I/V	11.7 (20.5)	9.2 (15.2)	10.5 (16.5)	12.0 (22.0)
Width peristome	9.0 (16.0)	9.4 (15.5)	7.5 (11.5)	7.0 (13.0)
Diameter periproct	6.3 (11.0)	8.4 (14.0)	8.5 (est)	8.8 (16.5)
Length labrum to ant.	8.2 (14.5)	11.4 (19.0)	11.2 (17.5)	10.0 (18.5)
No. genital pores	four	two	four	four
Nature of pore pairs in amb. III	double	double	single	single

teratological specimen. The adoral surface is malformed and the labrum is grossly misshapen (Fig. 10F). A singular feature is the presence of tuberculation on the periplastronal area. This region is virtually free of tuberculation in the holotype (Fig. 10D).

Genus *PRORASTER* Lambert 1895
[= *Hypselaster* Clark 1917]

Type species. Schizaster atavus Arnaud *in* Cotteau 1883, p. 13.

Remarks. Mortensen (1951, p. 228) characterized *Proraster* by its possession of a deep ambulacrum III, with deep anterior notch in the test; a peripetalous fasciole, but not lateroanal fasciole; and four genital pores. On the basis of this definition *Proraster* differs from *Schizaster* only in its lack of a lateroanal fasciole. The genus *Hypselaster* is here considered to be synonymous with *Proraster,* as the lateroanal fasciole is rudimentary or lacking. Mortensen (1951, p. 312) noted that *Hypselaster* is "an unsatisfactorily limited genus". He further observed that the lateroanal fasciole may be present in a rudimentary form or be entirely absent: yet he gave the main character of *Hypselaster* as the presence of a rudimentary fasciole. Five specimens in the Australian Museum collection (AM J6625) collected by H. L. Clark from Roebuck Bay, Broome, Western Australia, lack the lateroanal fasciole entirely, while one specimen shows a small segment ventro-lateral of the periproct. It straddles the junction of two interambulacral plates, indicating that it appeared in maturity and did not degenerate to this condition.

H. L. Clark (1917) also characterized *Hypselaster* by the possession of only two genital pores: *Proraster* has four. This difference is not considered to be sufficient to merit generic separation. Lambert's *Proraster* ranges from the Cenomanian to Senonian, whilst species referred to *Hypselaster* by H. L. Clark (1917) and Mortensen (1951) are all living species. Mortensen (1951, p. 313) tentatively placed *H. perplexus* Arnold and Clark (1927) in *Hypselaster;* this species is from the Eocene (?) of Jamaica.

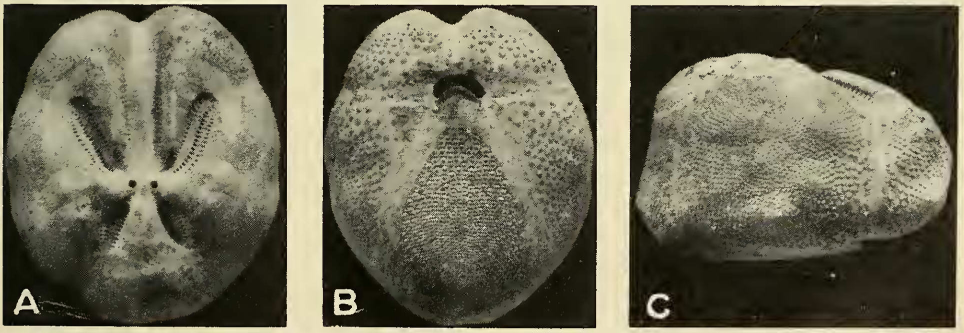


Fig. 11. Proraster jukesii (Gray 1851), AM J6625, from Roebuck Bay, Broome, Western Australia: A, aboral view; B, adoral view; C, lateral view, all x1.

Proraster jukesii (Gray 1851)
(Figs 11A-C, 12A)

1851 *Schizaster jukesii* Gray, p. 133
1855 *Schizaster jukesii* Gray, p. 61, Pl. 3, fig. 4
1925 *Hypselaster fragilis* Clark, p. 208, Pl. 11, figs 1-3
1938 *Hypselaster dolosus* Clark, p. 430, Pl. 28, figs 4-7
1946 *Hypselaster dolosus* Clark; Clark, p. 367
1951 *Hypselaster dolosus* Clark; Mortensen, pp. 319-320, Pl. 32, fig. 6

1951 *Hypselaster jukesii* (Gray); Mortensen, pp. 315-319, Pl. 22, figs 14-17, Pl. 52, figs 2, 9, 21, 22

1961 *Hypselaster jukesii* (Gray); Endean, p. 294

1972 *Hypselaster jukesii* (Gray); A. M. Clarke & Rowe, p. 167, footnote 16.

Type specimen. The specimen figured by Gray (1855, Pl. 3, fig. 4) and identified and figured by Mortensen (1951, p. 318, Pl. 22, figs 15-17) and in the collections of the British Museum (Natural History). It is from "Cape York".

Localities. Mortensen (1951, p. 316) gave the geographic range of *P. jukesii* as "from the Torres Strait region to the Queensland coast (Bowen)". H. L. Clark's "*H. dolosus*" was based on specimens from Broome and Augustus Island, Western Australia. Six specimens studied in this paper were collected by Clark from tidal falts at Roebuck Bay, Broome. Endean (1961, p. 294) records two specimens from Myora, Moreton Bay and four from Dunwich, Moreton Bay. These were taken at L.W.N. from sand flats.

Remarks. H. L. Clark (1946, p. 367) distinguished his Western Australian specimens from those from eastern Australia by the position of the apical system, which he considered to be slightly posterior of centre in the Western Australian form *P. "dolosus"* but anterior of centre in *P. jukesii*, and by differences in petaloid area and shape of the valve of the globiferous pedicellariae. Mortensen (1951, p. 318) further suggested that *P. "dolosus"* has narrower posterior paired petals than *P. jukesii.* A. M. Clarke and Rowe (1971, p. 167, footnote 16) have pointed out that neither of these supposed differences in test character is borne out by Mortensen's (1951, Pl. 22) illustrations of the species. We therefore follow these authors in placing *dolosus* in synonymy with *jukesii.*

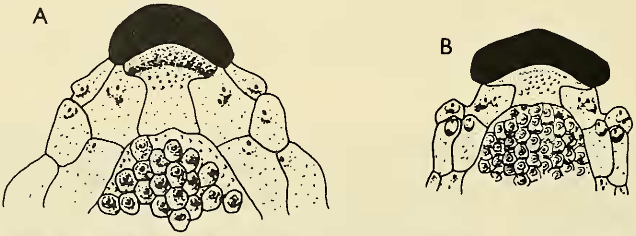


Fig. 12. Labrum and adjoining ambulacral plates of, A, *Proraster jukesii* (Gray 1851), AM J6625, from Roebuck Bay, Broome, Western Australia, x2.5; B, *Moira lethe* Mortensen 1930, QM G12093, from Moreton Bay, Queensland.

Globiferous pedicellariae are not common in *P. jukesii.* A Western Australian specimen shows the pedicellariae to have two teeth at the distal end as is typical. However, in comparison with Mortensen's illustration (Pl. 52, fig. 21) of a globiferous pedicellaria of *P. jukesii,* the Western Australian specimen has valves which are relatively longer. However, this is judged to be insufficient grounds to warrant the separation of the two forms as different species.

Genus *MOIRA* Agassiz 1872

Type species. Spatangus atropos Lamarck 1816, p. 32. By subsequent designation of the International Commission of Zoological Nomenclature; Opinion 209, 1948.

Moira lethe Mortensen 1930
(Figs 12B, 13A-D)

1926 *Moira stygia* Lütken, Clark, p. 191

1930 *Moira lethe* Mortensen, p. 392, Pl. 3, figs 1-4

1938 *Moira stygia* Lütken, Clark, p. 432

1946 *Moira stygia* Lütken, Clark, p. 369

1951 *Moira lethe* Mortensen; Mortensen, pp. 334-335, Pl. 19, figs 12, 18, 22; Pl. 55, figs 12, 24.

Localities. Mortensen (1951, pp. 334-335) records this species from Bowen, Queensland; "Liverpool, (!) N.S.W."; Broome, Western Australia; and South Australia. Specimens have also been found by one of us (K. J. McN.) on the eastern side of Bribie Island, Queensland and at Myora, Moreton Bay, Queensland. It is also known from Albany, Western Australia and from Port Phillip Bay, Victoria (A. M. Clarke, 1966, p. 292).

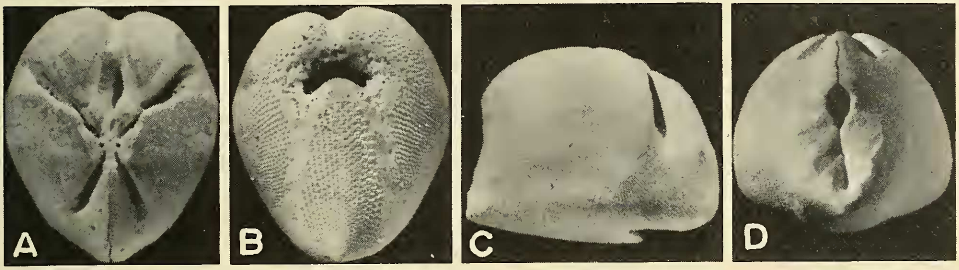


Fig. 13. Moira lethe Mortensen 1930, QM G12092, from Moreton Bay, Queensland; **A**, aboral view; **B**, adoral view; **C**, lateral view; **D**, posterior view; all x1.

As noted by Mortensen (1951, p. 334) this species is most similar to *M. stygia,* from which it can be distinguished by the deep, sagittal depression between the periproct and lowest part of the lateroanal fasciole (Fig. 13D), and by its shorter labrum (Fig. 12B).

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